THE NORTH AMERICAN ASCLEPIADACEAE

I. PERSPECTIVE OF THE GENERA

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INTRODUCTION

The problem of the North American genera of Asclepiadaceae has been summarized well by Standley (Fl. Costa Rica **3**: 949. 1938): "The family is noteworthy for the complicated structure of the flowers, more complicated, probably, than those of any other family of plants. The Mexican and Central American members of the group have never been monographed properly, and their classification is at present in a decidedly chaotic state."

It is unfortunate that Charles Darwin did not compose a study on the floral structure and pollination of Asclepiads as a companion to his famous observations on Orchids. In both groups, as distantly related as Dicotyledons and Monocotyledons may be, entomophily has produced elaborate and variable innovations from group to group. But apparently with the same intention: for the attraction of insects and crossfecundation by them, through means of a pollinium. The Orchids have responded to entomophily largely by zygomorphy and elaboration of the perianth. In the Asclepiads, on the other hand, actinomorphy has been retained, and, although corolline modifications are obvious, diversification is due chiefly to the structural plasticity of the staminal filaments. These elaborations of the stamens are known as the corona. Since the anthers of Asclepiads are invariably five in number, it obtains that the corona also is five-parted, the segments being quite free or mutually coherent, and diversified in ways that are too numerous for description. Although a staminal corona is the rule for the group, a few entities possess Issued April 28, 1941. (193)

194 ANNALS OF THE MISSOURI BOTANICAL GARDEN

simple filaments. In any event, the center of the flower is occupied by a composite structure known as the gynostegium, comparable to the column of Orchids. This consists of the five coherent stamens surrounding the style of the bicarpellate pistil, with an enlarged terminal "stigma head" at the free end. The whole stigma head is not truly stigmatic, the receptive surfaces being five narrow strips of glandular tissue be-

tween the contiguous anthers.

The anthers of American Asclepiads are bilocular, and within each cavity the pollen grains are grouped at maturity into a glutinous, sac-shaped pollinium of definite form and size. In the subfamily Cynanchoideae, containing all the New World species, these pollinia are combined by pairs through a more or less elaborate yoke mechanism called the translator. The translators consist of two arms^{*} attached to their respective pollinia, and are themselves joined by a roughly sagittate body called the "gland."^{*} A pair of pollinia, therefore, consists of the contents of adjacent anther cavities of contiguous anthers. The translators, with their glands, are formed between the neighboring anthers.

The current explanation of the formation of the translators

is that their substance consists of the solidified secretion of special glandular cells located upon the stigma head. Investigations of my own, not yet completed, lead me to assume that in the early development of the pollinia the tapetal liquid, characteristically abundant in young anthers, seeps through small pores of the neighboring anthers to gather in the commissural grooves of the two organs. This liquid later solidifies outside the anther as well as about the pollen, instead of being absorbed as is usually the case. Superficial support is given this view by the fact that the uniting "gland" always is distinctly 2-parted. According to either view, the translators are moulded when still in the liquid state by the available spaces between the young anthers.

* "Translator arm" and "gland" frequently are called "retinaculum" and "corpusculum" respectively in the literature. The former are chosen here as being somewhat more easily associated with the appearance of the structures as well as more adaptable to English: the latter are more useful in Latin diagnoses.

WOODSON—NORTH AMERICAN ASCLEPIADACEAE. I 195

When the pairs of pollinia are mature they are easily removed from the dehiscent anthers by means of the yoke-like translators. A visiting insect may be observed to pull them out and carry them away suspended from its legs. On the same or another flower, the pollinium must be inserted between the anthers at the stigmatic surface, in order to insure pollination. At that time, in response to the stigmatic secretions, pollen tubes germinate from the pollinium while still intact, to travel down the style to the ovules. The significance of the pollinia and their method of fecundation were fully appreciated for the first time by Robert Brown (Mem. Wern. Soc. 1: 12-58. 1809) in his celebrated paper distinguishing the Asclepiads from the Apocynads. The method of pollination in Asclepiads which Robert Brown disclosed appears at first sight to be of design so cunning that great fecundity of the plants should be assured, as well as frequent hybridization. Every conceivable innovation would seem to have been made by the flowers to insure successful insect ministrations. But such does not necessarily seem to have resulted. The family as a whole is outstanding for the constancy of its species and the rarity of obvious hybridity. Furthermore, the amount of fruit produced scarcely seems to be commensurate with the "efforts" taken to insure it, to speak anthropocentrically. Accounts of the pollination of Asclepiads seldom mention the actual difficulties intervening: the danger of the pollinia being broken or only partially withdrawn by the insect's casual visits; the horny margins of the anthers which seclude the stigma, frequently with entangling hooked or grooved decorations. Germinated pollinia are conspicuous, even in dried and boiled material, because of the abundant, felty pollen tubes. Amongst the hundreds of flowers of various genera and species which I have dissected under magnification, I have found very few indeed bearing germinated pollinia in the stigmatic chamber between the anthers. Of those few, the companion pollinium was usually in place in its mother anther sac. In nu-

196 ANNALS OF THE MISSOURI BOTANICAL GARDEN

merous instances I have found germinated pollinia while still within the anther sac. Whether such pollen tubes can reach the ovules successfully has not been ascertained, but it is not impossible. Such observations explain to some extent the rarity of hybridization, but fail to shed much light on the use of the pollinia as agents for pollination by insects.

Another feature of the Asclepiad flower which would appear to have little positive survival value is the division of the stigma into five rather restricted receptive regions. This apparently is responsible for the fact that only one follicle commonly develops from the two carpels of the pollinated pistil. Thus, even though three stigmatic surfaces were to receive pollinia, fecundation of only one carpel might result: but it must be confessed that conversely were only two pollinia deposited development of both follicles might ensue. A pair of follicles, nevertheless, is seldom encountered. Perhaps it is safe to assume that the reduction in number of fruits is compensated by the volatility of the comose seeds.

The classification of Asclepiadaceae into major divisions is based upon the nature and position of the pollinia, and thus owes its foundations to the classical observations of Robert

Brown (Mem. Wern. Soc. 1: 12-58. 1809). That versatile genius separated the family as it is now recognized into five tribes: Periploceae, with open cornucopia-shaped pollinia and adhesive translators somewhat as in the Orchids; Secamoneae, with 4-locular anthers, the yoke-like translators bearing two pollinia upon each arm; Asclepiadeae Verae, with 2locular anthers, the yoke-like translators bearing a single pendulous pollinium upon each arm; Gonolobeae, with pollinia similar to those of Asclepiadeae Verae, but horizontal; and Stapelieae, with similar, but erect pollinia. Recent systems (cf. K. Schumann, in Engl. & Prantl, Nat. Pflanzenfam. 4²: 209. 1895) have divided the family into two subfamilies, Periplocoideae and Cynanchoideae; the latter having four tribes, Asclepiadeae, Secamoneae, Tylophoreae (Stapelieae of Brown), and Gonolobeae. In the New World only the Cynanchoideae are encountered in the native flora, with the three tribes Asclepiadeae, Gonolobeae, and Tylophoreae.

WOODSON-NORTH AMERICAN ASCLEPIADACEAE. I 197

In these studies no attempt will be made to subdivide the tribes into the smaller subdivisions advocated by Schumann, for these are manifestly unnatural. Thus the genus Sarcostemma R.Br. (sensu stricto) was placed in the subtribe Cynanchinae of Asclepiadeae by that author (K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4²: 245. 1895), but the two certainly synonymous genera, Philibertia HBK. and Funastrum Fourn., in the Glossonematinae and the Asclepiadinae respectively (pp. 225, 231. loc. cit.). I am inclined also to ignore Schumann's subtribe Astephaninae, characterized by the absence of a corona, since in all cases which I have observed the absence of a crown is the only character separating species groups of obviously close affinity, notably in the inclusive treatment of Cynanchum adopted here. One monotypic genus, Tylodontia Griseb. (treated as a division of Cynanchum here), Schumann includes in the Astephaninae, but I have observed the presence of definite corona segments in an isotype deposited in the herbarium of the Missouri Botanical Garden (Wright 2964). Neither can Oxypetalinae of Schumann be maintained by the appendages of the translator arms, since several South American species of the single genus, Oxypetalum, do not have those

structures.

The separation of the American Asclepiads into tribes sometimes is a bit difficult, since the position of the pollinia usually must be observed while they are still within the anther sac. Once withdrawn and placed upon the dissecting stage, the delicate translator arms are apt to twist into any conceivable attitude, frequently giving a false impression of their natural position. The Asclepiadeae and Tylophoreae usually are quite easy to detect; but the Gonolobeae have given trouble from the start. I am willing to be convinced that the normal position of the Gonoloboid pollinium may be truly horizontal, although my interpretation of the tribe includes forms with pollinia that range in position from pendulous to ascending. By far the best means that I have found to separate this tribe is by means of

the structure, not the position, of the pollinia.

In all the Asclepiadeae and Tylophoreae examined by me, the faces of the pollinium are uniformly rounded or flattened on

t t

198 ANNALS OF THE MISSOURI BOTANICAL GARDEN

either side, and the translator arm makes a sharply definite connection with them. In the Gonolobeae, on the other hand, the faces of the pollinium are more or less dissimilar: one convex or rounded and the other flattened or somewhat excavated, frequently very strikingly so. In some cases both sides are deeply furrowed or excavated. In the Gonolobeae, also, the translator arm usually engages the pollinium more gradually, the attachment being marked by a more or less conspicuous hyaline indentation or margin (always the upper). Without the use of this structural criterion, Schumann placed such genera as Macroscepis and Fischeria in the Asclepiadeae and Metalepis in the Gonolobeae, whereas other characters of the plants show their natural positions to be exactly the reverse, as shall be explained presently. At this writing ninety-seven genera of Asclepiadaceae have been described from North America, based wholly or in large part upon the structure of the corona. Authors of the great majority of these genera seem not to have understood what a versatile feature this organ is, for it is only when its multifarious aspects are interpreted in a broad and comparative manner that a natural and conveniently referable classification can result. North American students of tropical Asclepiads, particularly, would do well to consider the floral variability of the native Milkweeds before attempting the description of exotic genera. The prospective Asclepiadologist should understand from the first that differences of the corona separate species in this family, which would form remarkable generic criteria, say of the "disc" in other families. After the first shock of surprise at the few genera recognized for North America, readers of the following key to genera may notice the fairly incidental use of corona characters. These are reserved chiefly for subgeneric and sectional distinctions, and will be discussed in that connection.

The term "corona" has been taken in a rather restricted sense in these studies. Amongst earlier literature frequent mention is made of "double" or even of "triple" coronas. This terminology is very confusing except to the authors concerned. Morphologically, the corona, as interpreted here,

WOODSON—NORTH AMERICAN ASCLEPIADACEAE. I 199

consists of various elaborations or enations of the staminal filaments only. These enations may occur as separate bodies attached to the staminal column, as in Asclepias, to cite a familiar example, or may consist of a more or less entire ring of tissue adnate to the bases of both staminal column and corolla throat. Where "double" or "triple" coronas have been described by various authors, these usually will be found to consist of a faucal annulus of the corolla tube, or sterile appendages of the anthers, which are rather to be called such than to be referred to as corona. The most cogent reason for avoiding the use of "corona," except in a simple sense, is that many readers of the literature are apt to interpret a corona as double, whilst the author may not intend such a view. Several instances of possible or published confusion arising from an author's use of "double corona'' come to mind. In the subgenus Chthamalia of Matelea, for example, the corona consists of an annular structure of five more or less united and variously constituted segments, each of which bears internally a more or less conspicuous ligular process, sometimes surpassing the height of the subtending segment. Contrary to what one might suppose, this complex structure is not considered by the literature as a "double corona." The flowers of Gonolobus (sensu stricto) are very difficult to identify with standard keys, for they usually possess (1) a faucal annulus of the corolla, (2) a fleshy, true corona, (3) dorsally appendaged anthers. Some authors interpret these structures as constituting a "triple" and some as a "double" corona. Those maintaining the dual nature may construe either the corolline annulus or the anther appendages as the supernumerary corona, in which cases the true corona will be spoken of as either the "inner" or the "outer" corona, respectively.

The segregate genus *Podostigma*, of the southeastern United States, is keyed by K. Schumann (in Engl. & Prantl, Nat. Pflanzenfam. 4^2 : 235. 1895) on the basis of having an "inner corona" borne high upon the column, alternate with the anthers. When these tiny objects are examined, however, they are found to be nothing but the minute ligules commonly alter-

200ANNALS OF THE MISSOURI BOTANICAL GARDEN

nating with the corona hoods in Asclepias proper, their normal position doubtless having been disturbed by the elongation of the anther stipe* above the insertion of the hoods. In Fischeria, also a "double corona" is described in all texts. But when carefully dissected, the bladder-like "inner corona segments" are found to be nothing but the hypertrophied anthers themselves. This peculiar mark of Fischeria may be described more accurately and more clearly upon the basis of anther structure than by introducing an ambiguous and morphologically indefensible reference to supposed "corona." The North American Asclepiadaceae have never had the attentions of a specialist devoted primarily to their study, except for the period between 1897 and 1904 during which a series of eight short papers by Miss Anna Murray Vail appeared in the 'Bulletin of the Torrey Botanical Club.' These papers consist only of short notes, with the exception of rather casual revisions of Acerates, the Asclepias verticillata complex, and Rouliniella (i.e. Cynanchum subgenus Mellichampia, in part, of my studies). Even from these small and interrupted beginnings, it is obvious that Miss Vail possessed a very considerable knowledge and insight into the North American Asclepiads, and it is regrettable that her retirement to France terminated her ambitions for more comprehensive works. I must confess that more than once, when I was apparently undergoing swift mental attrition because of the damnably variable coronas and pollinia, I have reflected on my predecessor's retreat to the Riviera. The South American and Antillean Asclepiads have had several specialists, including Decaisne, Fournier, Schlechter, and Malme; to these must be added the contemporary South American botanists, A. G. Schulz and F. C. Hoehne. The work of these eminent systematists, however, has nearly always been in the field of regional floristics, with few exceptions, such as Malme's monograph and subsequent emendations on Oxy-

* I have found it convenient in dealing with some genera to distinguish two regions of the staminal column: that below the attachment of the corona as the "column," as in most species of Asclepias proper, and that above, between the corona and the anthers proper, as the "stipe," as in Podostigma.

WOODSON-NORTH AMERICAN ASCLEPIADACEAE. I 201

petalum. But these contributions have affected the northern Asclepiads only in rather minor particulars. Regional floras of North America have included thoughtful interpretations of the Asclepiadaceae in several instances, but have been hindered by their restricted scope and the divided interest of their authors.

Special mention should be made here to the monograph of

Marsdenia by Rothe (in Engl. Bot. Jahrb. 52: 354–434. 1915), not only since it is the only comprehensive account of an Asclepiad genus in both American continents, but because the author's solution of the problems of this group closely parallel my own for the family. Confronted by an aggregation of eight segregate genera, nearly all in current use but with very evasive criteria when seen as a whole, Rothe courageously combined them as sections. The result, in spite of some imperfections, is the one bright spot in the determination of tropical American Asclepiads from the existing literature. In the Tylophoreae, at least, one needs no longer to puzzle over the generic interpretation of floral innovations, nor fear that the specimen he is trying to determine may already be described as a new genus in some remote section of the taxonomic indices.

At the same time, a natural system of species groups is defined and provided with names which may (or should) be used in the description of novelties, or to which additions may even be made should sufficiently discrepitant plants be found.

A lifetime would be too short to perfect a complete system of the North American Asclepiads. But after an intensive study of several years, I have arrived at a definition of the genera which I believe may well lead to a more adequate understanding of the complex as a whole. The result is a revolutionary change in nomenclature which surely will not be regretted more by the reader than by the author. The change clearly is unavoidable because of the long neglect of the family.

In this group of plants apparent entomophily has produced a floral structure even more complicated and variable than in the Orchids. Morphological details separate species and even varieties here, which would serve to distinguish genera in other groups of Flowering Plants. The student of the Asclepiads is

202 ANNALS OF THE MISSOURI BOTANICAL GARDEN

impelled to the defeatist attitude that only two choices are available in classification: to "lump" genera or to "split" them. If he continues the study of Milkweeds sufficiently long, he probably will find himself tossed from horn to horn of the dilemma.

After several such harrowing experiences, I have recognized that a narrow concept of coronal structure as a criterion of genera, if pursued consistently, will lead to a multitude of monotypic entities—as a matter of fact, that few genera will consist of more than two or three species—and that each new species will introduce anew the question of generic differentiation. This is scarcely an exaggeration when one remembers that an inclusive concept of North American Asclepias, alone, involves the listing of twenty generic synonyms. If he contemplates an extended association with the Asclepiadaceae, with yearly increments of specimens brought to his attention for classifying, even the most hardened "liberal" taxonomist will take heed before embarking upon such a disastrous course. Although the results of my studies wreak havoc upon the existing classification, I feel confident that the groups proposed are natural, and that they will stand the test of many

years. The desideratum of stability and convenience will be served much better in having a few, almost infallibly recognizable genera even though they may be large: the natural affinities within these groups may be indicated sufficiently by the erection of subgenera and sections.

This paper is intended as the forerunner of a series devoted to the North American Asclepiadaceae. It is composed as a general survey of the generic elements involved, together with an indication of representative changes in nomenclature made necessary by my visualization of the natural system of the family. These species are drawn only from those with which I am familiar at this time, and should not be considered as complete synopses; neither do they include species not requiring adjustment in terminology. The synonymy, also, is not complete, consisting merely of the name-bringing and other more prominent synonyms. To some readers, the inclusion of the many nomenclatural changes upon such a scanty prepara-

WOODSON-NORTH AMERICAN ASCLEPIADACEAE. I 203

tion may seem precipitate. The decision to include them here, rather than to withhold them for subsequent, complete revisions, has been made in view of the advantages of concrete illustration of the generic elements proposed, the uncertainty of our ability to obtain European types necessary for a complete study within the near future, and the validation of obviously necessary names for the purpose of present determinative work. Should the future permit, this paper will be followed by a monograph of the North American species of Asclepias, and by subsequent revisions of the other important genera, in each case with all recognized species illustrated by analytical drawings. To be of wide use, a critical study of the Asclepiadaceae should be illustrated profusely. I feel that an apology is in order, therefore, because of the total lack of analytical drawings in this paper. Their absence is due in part to the conditions of publication at the moment, and in part to plans which I have made for their inclusion in future studies. After all, this paper is scarcely more than an annotated key to genera, and of little interest save to specialists. Such readers will be sufficiently familiar with the structures to which I call atten-

tion not to miss the figures.

KEY TO THE TRIBES AND GENERA

ASCLEPIADEAE

Erect or decumbent perennial herbs; pollinia very strongly flattened; corona of 5 cucullate, calceolate, or clavate hoods, usually with an internal horn or crest.....I. ASCLEPIAS

Lianas or twining undershrubs; pollinia faces broadly rounded or only slightly compressed.

204ANNALS OF THE MISSOURI BOTANICAL GARDEN

Arms of translators not as above.

Corona of 5 separate or united, laminate to filiform scales, occasionally compounded or with internal processes, rarely wholly lacking......III. CYNANCHUM Corona of 5 semi-vesicular sacs attached separately to the backs of Corona of 5 closed inflated vesicles joined at the bases by a fleshy

GONOLOBEAE

Anthers relatively simple, not conspicuously vesicular, nor with dorsal ap-Anthers very conspicuously hypertrophied and vesicular throughout; corolla Anthers with spreading, more or less laminate, fleshy dorsal appendages;

TYLOPHOREAE

I have been unable to interpret two enigmatic genera of Baillon, Microstelma (Hist. Pl. 10: 286. 1891) and Stelmagonum (loc. cit. 287), both placed in the Gonolobeae and thus probably synonymous under Matelea.

I. ASCLEPIAS L. Sp. Pl. 214. 1753.

Anthanotis Raf. Fl. Ludov. 52, 149. 1817. Anantherix Nutt. Gen. N. Am. Pl. 1: 169. 1818. Stylandra Nutt. loc. cit. 170. 1818. Otaria HBK. Nov. Gen. 3: 192. 1819. Acerates Ell. Sketch Bot. S. Carol. 1: 316. 1821. Podostigma Ell. loc. cit. 326. 1821. Acerotis Raf. New Fl. N. Am. 1: 49. 1836. Oligoron Raf. loc. cit. 4: 60. 1836. Otanema Raf. loc. cit. 61. 1836. Onistis Raf. loc. cit. 63. 1836.

Polyotus Nutt. Trans. Amer. Phil. Soc. n.s. 5: 199. 1837. Asclepiodora A.Gray, Proc. Amer. Acad. 12: 66. 1877.

WOODSON-NORTH AMERICAN ASCLEPIADACEAE. I 205

Schizonotus A.Gray, loc. cit. 1877, non Lindl.
Solanoa Greene, Pittonia 2: 67. 1890.
Solanoana O.Ktze. Rev. Gen. 2: 421. 1891.
Oxypteryx Greene, Pittonia 3: 234. 1897.
Podostemma Greene, loc. cit. 235. 1897.
Biventraria Small, Man. Fl. 1072. 1933.
Asclepiodella Small, loc. cit. 1073. 1933.

Gomphocarpus of American authors.

Key to the Subgenera

- A. Corolla rotate to rotate-subcampanulate, the lobes reflexed to somewhat ascending; corona attached to the column immediately beneath the anther head.
 - B. Hoods cucullate or cucullate-spatulate to calceolate, rarely strongly conduplicate, erect to spreading, the alternate lobules more or less deeply 2-cleft, rarely absent.
 - C. Corolla throat without internal callous processes.
 - DD. Hoods very sessile, the basal attachment deeply saccate.
 - E. Hoods entire to somewhat cleft ventrally, open but occasionally appressed against the column.
 - F. Base of hoods not appendiculate, or merely somewhat keeled
 - laterally.
 - G. Hoods with a more or less conspicuous internal horn or crest.

BB. Hoods thickly involute-clavate.

206 ANNALS OF THE MISSOURI BOTANICAL GARDEN

[VOL. 28

This key will not be of great use to those who are not thoroughly familiar with the varying structure of the Milkweed flower. The monograph of the genus which I am preparing will contain the discussion and illustrations of the criteria necessary for general use.

To many readers familiar with the segregate genera of Asclepias in a restricted region of the United States, the reduction of such well-established entities as Acerates, Asclepiodora, and Podostigma may appear as an admission of casual superficiality. Let them study the scores of species of Asclepias represented in North America, intensively, for several years, however (and above all, let them attempt to compose an adequate key even to subgenera and sections), and I am convinced that those without prejudice will appreciate the practical and theoretical advantages of "lumping." Fortunately, very few new combinations are necessary by interpreting the genus in a broad sense, for practically all species have been described under Asclepias at one time or another. The relatively few exceptions amongst the species with which I am familiar at present are treated under their respective subgenera as follows:

SUBGENUS 1. EUASCLEPIAS

ASCLEPIAS hypoleuca (A.Gray) Woodson, comb. nov. Gomphocarpus hypoleucus A.Gray, Proc. Amer. Acad. 17: 222. 1881–82.

ASCLEPIAS Phenax Woodson, nom. nov.

Acerates humilis Benth. Pl. Hartw. 291. 1848, non Asclepias humilis Schltr.

ASCLEPIAS Pringlei (Greenm.) Woodson, comb. nov.

Acerates Pringlei Greenm. Proc. Amer. Acad. 34: 570. 1899.

207 WOODSON-NORTH AMERICAN ASCLEPIADACEAE. I

SUBGENUS 5. ACERATES

ASCLEPIAS hirtella (Pennell) Woodson, comb. nov. Acerates hirtella Pennell, Bull. Torrey Club 46: 184. 1919.

SUBGENUS 6. POLYOTUS

ASCLEPIAS Engelmanniana Woodson, nom. nov. Acerates auriculata Engelm. in Torr. Rept. Bot. Mex. Bound. Surv. 160. 1859.

Asclepias auriculata (Engelm.) Holzinger, Bot. Gaz. 17: 125, 160. 1892, non HBK.

SUBGENUS 7. SOLANOA

ASCLEPIAS Solanoana Woodson, nom. nov.

Gomphocarpus purpurascens A.Gray, Proc. Amer. Acad. 10: 76. 1874, non A.Rich.

Schizonotus purpurascens A.Gray, loc. cit. 12: 66. 1877. Solanoa purpurascens (A.Gray) Greene, Pittonia 2: 67. 1890.

Solanoana purpurascens (A.Gray) O.Ktze. Rev. Gen. 2: 421. 1891.

SUBGENUS 8. ASCLEPIODOLUS

ASCLEPIAS insignis (Brandg.) Woodson, comb. nov. Asclepiodora insignis Brandg. Zoe 5: 253. 1908. SUBGENUS 10. ASCLEPIODORA ASCLEPIAS circinalis (Dene.) Woodson, comb. nov. Acerates circinalis Dene. Ann. Sci. Nat. Bot. ii. 9: 322. pl. 10, fig. c. 1838. Asclepiodora circinalis (Dene.) Fourn. loc. cit. vi. 14: 369. 1882.ASCLEPIAS Fournieri Woodson, nom. nov. Acerates gomphocarpoides Dene. Ann. Sci. Nat. Bot. ii 9: 323. 1838, non Asclepias gomphocarpoides Schltr. Asclepiodora gomphocarpoides (Dcne.) Fourn. loc. cit. vi. 14: 369. 1882. ASCLEPIAS zanthodacryon (Smith & Harris) Woodson, comb.

nov.

Asclepiodora zanthodacryon Smith & Harris, Contr. Gray Herb. 114: 12. 1936.

208ANNALS OF THE MISSOURI BOTANICAL GARDEN

II. OXYPETALUM R.Br. Mem. Wern. Soc. 1: 41. 1809.

Apparently O. cordifolia (Vent.) Schltr. is the only representative of this troublesome genus in Central America and the Antilles. Fortunately, this species has strongly appendaged translator arms which enable it to be separated easily from Cynanchum. But in South America there are many species without this diagnostic structure, the importance of which will

present one of the major problems of the Asclepiads in the southern continent.

III. CYNANCHUM L. Sp. Pl. 212. 1753.

Ditassa R.Br. Mem. Wern. Soc. 1: 49. 1809. Metastelma R.Br. loc. cit. 52. 1809. Enslenia Nutt. Gen. N. Am. Pl. 1: 164. 1818, non Raf. Ampelamus Raf. Amer. Monthly Mag. 4: 192. 1819. Lyonia Ell. Sketch Bot. S. Carol. 1: 316. 1821, non Nutt. Seutera Reichenb. Consp. 131. 1828. Enslinia Reichenb. loc. cit. 1828. Roulinia Dene. in DC. Prodr. 8: 516. 1844, non A. Brongn. Orthosia Dene. loc. cit. 526. 1844.

Tassadia Dene. loc. cit. 579. 1844. Irmischia Schlecht. Linnaea 19: 738. 1847. Nanaturis Turcz. Bull. Soc. Nat. Mosc. 21¹: 254. 1848. Amphistelma Griseb. Fl. B.W.I. 417. 1861. Tylodontia Griseb. Cat. Pl. Cub. 175. 1866. Metalepis Griseb. loc. cit. 179. 1866. Mellichampia A.Gray, Proc. Amer. Acad. 22: 437. 1887. Pattalias S.Wats. loc. cit. 24: 60. 1889. Tainionema Schltr. in Urb. Symb. Ant. 1: 263. 1899. Decastelma Schltr. loc. cit. 264. 1899. Rouliniella Vail, Bull. Torrey Club 29: 662. 1902. Basistelma Bartlett, Proc. Amer. Acad. 44: 631. 1909. Epicion Small, Man. Fl. 1075. 1933. Astephanus of American authors.

Besides the preceding, several synonyms eventually will have to be added from the South American flora. Very few of

WOODSON-NORTH AMERICAN ASCLEPIADACEAE, I 209

1941]

these synonymous genera are absolutely co-extensive, since they are based for the greater part upon variations of the corona. Because these differences are multitudinous but of the same general motif, the practical solution of the problem appears to lie in an inclusive treatment, such as that adopted for Asclepias. The principal characters used to separate the segregates just enumerated are aestivation of the corolla lobes (whether contorted or valvate—extremely difficult to observe in most species), corona (whether simple or compound, deeply or less deeply divided, or absent), and structure of the inflorescence (whether racemiform or umbelliform-since the basic structure is cymose for all, this distinction resolves itself into a comparison of internode length). These characters combine kaleidoscopically in so many manners, and frequently result in the separation into different genera of so many species of obvious affinity, that they appear of very doubtful value. I am inclined to discount particularly the value of corolla aestivation and corona structure, and to group the North American species under the following subgenera. These I am illustrating with representative adjustments in nomenclature.

Key to the Subgenera

- A. Cymes racemiform to corymbiform, with definitely manifest internodes.
- B. Corolla campanulate to rotate-subcampanulate, the throat not constricted at the orifice.

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SUBGENUS 1. MELLICHAMPIA

Сумансним jaliscanum (Vail) Woodson, comb. nov. Rouliniella jaliscana Vail, Bull. Torrey Club 29: 668. 1902.

210 ANNALS OF THE MISSOURI BOTANICAL GARDEN

Сумансним jamaicense (Griseb.) Woodson, comb. nov. Enslenia jamaicensis Griseb. Fl. B.W.I. 418. 1861. Rouliniella jamaicensis (Griseb.) Rendle, Journ. Bot. 74: 340. 1936.

Сумансним lignosum (Vail) Woodson, comb. nov. Rouliniella lignosa Vail, Bull. Torrey Club 29: 666. 1902. Сумансним ligulatum (Benth.) Woodson, comb. nov. Enslenia ligulata Benth. Pl. Hartw. 290. 1848. Mellichampia rubescens A.Gray, Proc. Amer. Acad. 22: 437. 1887.

Ampelamus ligulatus (Benth.) Heller, Contr. Herb. Franklin & Marshall Coll. 1: 79. 1895.
Mellichampia ligulata (Benth.) Vail, Bull. Torrey Club 26: 425. 1899.

Roulinia ligulata (Benth.) Pittier, Contr. U.S. Nat. Herb. 13: 111. 1910, as to synonymy.

Сумансним Rensoni (Pittier) Woodson, comb. nov.

Roulinia Rensoni Pittier, Contr. U.S. Nat. Herb. 13: 101. 1910.

Сумансним saepimentorum (Brandg.) Woodson, comb. nov. Vincetoxicum saepimentorum Brandg. Univ. Cal. Publ.

Bot. 4: 381. 1913. Сумансним sinaloense (Brandg.) Woodson, comb. nov. Roulinia sinaloensis Brandg. Zoe 5: 243. 1908. Mellichampia sinaloensis (Brandg.) Kearney & Peebles, Journ. Wash. Acad. Sci. 29: 488. 1939. Сумансним unifarium (Scheele) Woodson, comb. nov. Gonolobus unifarius Scheele, Linnaea 21: 760. 1848. Roulinia unifaria (Scheele) Engelm. in Torr. Rept. Bot. Mex. Bound. Surv. 160. 1859. Rouliniella unifaria (Scheele) Vail, Bull. Torrey Club 29: 663. 1902.

CYNANCHUM Watsonianum Woodson, nom. nov.
Roulinia Palmeri S.Wats. Proc. Amer. Acad. 18: 115.
1883, non Cynanchum Palmeri (Wats.) Blake (Pattalias Palmeri Wats.).
Rouliniella Palmeri (S.Wats.) Vail, Bull. Torrey Club 29: 664. 1902.

WOODSON-NORTH AMERICAN ASCLEPIADACEAE. I 211

Ampelamus, Rouliniella, and Mellichampia can be recognized as genera only by extremely tenuous criteria. As far as I am aware, the first would have to be supported by the bifid corona segments and the rostrate stigma head; the second by a flat (or scarcely conical) stigma head and acuminate crown segments, although they are slightly emarginate in some species and not infrequently show a tendency toward the development of marginal lobules; the third would have to depend upon somewhat larger flowers than Rouliniella, somewhat more nearly campanulate corollas, and crown segments somewhat more united at the base. Mellichampia also has a stigma head intermediate between that of Ampelanus and that of Rouliniella. The crown segments of Ampelamus and of Mellichampia are flat; those of Rouliniella are usually somewhat cucullate or infolded at the base. The primary division of the key to subgenera advocated here is one that will have to be used in some cases with a certain degree of experience, if not prejudice. Whilst the inflorescence of the Mellichampia-complex may be described as racemiform generally, and that of the Metastelma-complex as umbelliform, ambiguous species occur in both groups quite frequently enough to support my contention that it is impractical to maintain a series of distinct genera. Whilst the flowers of the Mellichampia-complex are smaller, as a rule, than those of the Metastelma-complex, this is in the nature of a guiding "prejudice'' only. I have been unable to discover supporting structural characters of merit.

SUBGENUS 2. AMPELAMUS

CYNANCHUM LAEVE (Michx.) Pers. Syn. 1: 274. 1805.
Gonolobus laevis Michx. Fl. Bor. Am. 1: 119. 1803.
Enslenia albida Nutt. Gen. N.Am. Pl. 1: 165. 1818.
Ampelanus albidus (Nutt.) Britton, Bull. Torrey Club 21: 314. 1894.

The interpretation of this species has been singularly con-

fused. In 1803 Michaux (loc. cit.) founded *Gonolobus* with three species, two of which previously had constituted the whole complement of the earlier genus *Vincetoxicum* Walt.

212 ANNALS OF THE MISSOURI BOTANICAL GARDEN

(Fl. Carol. 104. 1788): G. macrophyllus (V. gonocarpos Walt.), and G. hirsutus (V. acanthocarpus Walt.). The third species, G. laevis, originated with Michaux.

It is important in this connection to emphasize certain morphological characters of the fruit as embodied in the generic and specific descriptions by Michaux. For the genus as a whole: "Folliculi plerumque costati seu angulosi..." The follicles of the three species were described as follows: G. macrophyllus-"folliculis costato-angulosis"; for G. hirsutus—"folliculis oblongis, sparsim muricatis"; but for G. laevis—"folliculis laevibus." It is obvious that the smooth condition of the fruit of G. laevis—not angled as in macrophyllus, nor muricate as in hirsutus—was particularly outstanding in the estimation of Michaux, and that it suggested the specific adjective itself. The type specimens of G. *laevis*, if they may be called such, have been examined both by Dr. Gray (Proc. Amer. Acad. Sci. 12: 75. 1877) and by Miss Vail (Bull. Torrey Club 26: 427. 1899), and both agreed that at least two elements are represented amongst the fragments, namely, flowers and angled fruits of G. suberosus (L.) R.Br.—of which G. macrophyllus Michx. (G. gonocarpos (Walt.) Perry) probably is no more than a variety—and leaves of the slender vine currently known as Enslenia albida Nutt. or Ampelanus (correctly Ampelanus) albidus (Nutt.) Britton. But Dr. Gray chose the flowers and fruit as authentic, whilst Miss Vail chose the leaves. At first glance Miss Vail's selection may appear to be with little foundation, until it is recalled that Michaux stipulated for his species "folliculis laevibus," exactly the condition of Ampelamus; and that in choosing the material with angled pods, Dr. Gray denied the diagnostic character of the species. In such an instance, of obviously accidental mixture, the evident solution is to accept, as typical, material known to coincide with the original literature.

Had she studied her problem under existing rules of nomen-

clature, Miss Vail certainly would have placed *laevis* in a new combination under *Ampelamus*. Under the interpretations current at the New York Botanical Garden during that

WOODSON-NORTH AMERICAN ASCLEPIADACEAE. I 213

time, however, she invoked the "Doctrine of Residues," returning G. macrophyllus and G. hirsutus to Vincetoxicum Walt., from which they had been taken by Michaux, and retaining the name Gonolobus for G. laevis.

In this connection, however, it should be noted that Michaux embodied in his diagnosis of *Gonolobus* two characters which do not coincide with the present interpretation of *G. laevis*:

"Stylus discoideo-5-gonus. . . Folliculi plerumque costati seu angulosi." The absence of a "Doctrine of Residues" notwithstanding, therefore, I feel that Miss Perry (Rhodora 40: 283. 1938) is quite correct in considering the Walterian element as typical of Gonolobus, choosing G. macrophyllus as the standard species. Nevertheless, one feels that sentiment may have induced her to perpetuate Dr. Gray's interpretation of G. laevis rather than the more logical conclusion of Miss Vail.

Although it does not bear directly upon the question of G. laevis, it might be well to explain here, for future reference, that although Vincetoxicum Walt. clearly antedates Gonolobus Michx., as well as Vincetoxicum Moench (Meth. 717. 1794), the nomenclatorial powers at Kew, invoked by Miss Perry (loc. cit. 281–282. 1938), "temporarily" have placed Vincetoxicum Moench on the list of Nomina Conservanda, tantamount to final acceptance, since "the European Vincetoxicum is so widely used that there is every chance of its being conserved" (passage of letter by Mrs. T. A. Sprague, as quoted by Miss Perry). I suspect that the European Asclepiadologists, having had Vincetoxicum Moench conserved for them, will scarcely know how to use it: its distinction from Cynanchum is extremely evasive.

SUBGENUS 3. METALEPIS

CYNANCHUM cubense (Griseb.) Woodson, comb. nov. Metalepis cubensis Griseb. Cat. Pl. Cub. 179. 1866. The inclusion of Metalepis within the Gonolobeae by Schumann (in Engl. & Prantl, Nat. Pflanzenfam. 4²: 297. 1895) is a conspicuous instance of the ambiguity of the current definitions of the tribes of Asclepiadaceae. The pollinia in the species of this subgenus are quite pendulous, with the equally

214 ANNALS OF THE MISSOURI BOTANICAL GARDEN

rounded surfaces characteristic of the Asclepiadeae, but the translators are very long and horizontal, a condition found exactly duplicated in a few species of the subgenus Mellichampia. Aside from this character, the subgenus depends upon the racemiform inflorescences and the cyathiform corona, the inadequacy of which, as generic characters, has been noted previously.

SUBGENUS 4. TYLODONTIA

Сумансним Grisebachii (Maza) Woodson, comb. nov. Tylodontia cubensis Griseb. Cat. Pl. Cub. 179. 1866, non Cynanchum cubense (Griseb.) Woodson (Metalepis cubensis Griseb.).

Astephanus Grisebachii Maza, Cat. Periant. 276. 1894. Tylodontia has been included as a synonym under Astephanus by Schumann (in Engl. & Prantl, Nat. Pflanzenfam. 42: 224. 1895), but dissection of flowers from an isotype (Wright 2964) in the herbarium of the Missouri Botanical Garden shows the presence of a corona of five erose, truncated scales. The subgenus is outstanding in the Mellichampia-complex because of the small flowers having urceolate corollas with sharply reflexed lobes.

SUBGENUS 5. METASTELMA

At present I do not feel sufficiently familiar with the synonymy of Metastelma to attempt the many nomenclatural changes necessary for inclusion in Cynanchum. This is the most difficult of the American groups of Asclepiads because the flowers are so small. Within the tiny corollas, averaging only about 2 mm. in length, are packed as many structural details and variations as within the larger flowers of other genera. Once when I was complaining to Dr. Standley of the eye and nerve strain necessary in dealing with the group, he laughingly agreed that it should be studied by an algologist or a mycologist.

Metastelma will be handled very much easier, I believe, if it is treated as a single subgenus under Cynanchum. Unquestionably the various entities included here are much more closely related to one another than to any other complex. The

WOODSON-NORTH AMERICAN ASCLEPIADACEAE. I 215

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whole aspect of the plants is so unmistakable that I feel, even with convenience particularly in mind, that "lumping" is natural as well.

As has been remarked in a previous paragraph, Astephanus is difficult to maintain upon a sure foundation even with the higher powers of a binocular dissecting microscope. Amongst several specimens ascribed to A. pubescens Greenm. in the herbarium of the Missouri Botanical Garden are two entities, one with a manifest corona and one without, the anthers of the two species differing considerably; yet the superficial aspects of the plants are all but undistinguishable. Natural genera should not be so easily confused. Many readers may be surprised at the inclusion of Ditassa and Decastelma with Metastelma. But the cleaving of the corona scales or the presence of a ventral tooth or ligule, which distinguish these entities from Metastelma (sensu stricto), are found amongst the Old World Cynancha as well as in the Mellichampia-complex of Central America. Similar variation also is found in Asclepias.

SUBGENUS 6. CLEISTOLOBUS

CYNANCHUM utahense (Engelm.) Woodson, comb. nov. Astephanus utahensis Engelm. Amer. Nat. 9: 349. 1875. The inflexed-cucullate corolla lobes of this species, unlike those of any other known to me, were interpreted by Dr. Engelmann as a modification to compensate for the absence of a corona.

IV. BLEPHARODON Dcne. in DC. Prodr. 8: 603. 1844.

The nine species assigned to Blepharodon by Decaisne fall into two groups superficially marked by volubile or erect herbaceous habits, but accompanied by interesting differences in the corona and pollinia as well. Although I may seem inconsistent in view of my treatment of generic lines generally in this family, I feel that two distinct genera may be represented. The North American species are all of the volubile group (with the exception of B. nerifolium Done., which I believe

216 ANNALS OF THE MISSOURI BOTANICAL GARDEN

probably will be found to be an Asclepias when the material is available for study), and since this group seems to have been more typical of the genus in the opinion of Decaisne, I am reserving the use of the generic name for that connection. In respect for the memories of the many genera that I have reduced to synonymy during these studies, I am deferring judgment on the generic status of the erect species until I have the opportunity to devote my attention to the South American Asclepiads.

V. SARCOSTEMMA R.Br. Mem. Wern. Soc. 1: 50. 1809. Philibertia HBK. Nov. Gen. 3: 195. 1819. Pentagonium Schauer, Nova Acta Acad. Caes. Leop. Nat. Cur. 19. Suppl. 1: 364. 1843. Zosima Phil. Sert. Mendoz. Alt. 29. 1871. Funastrum Fourn. Ann. Sci. Nat. Bot. vi. 14: 388. 1882. Cystostemma Fourn. in Mart. Fl. Bras. 64: 204. 1885. Philibertella Vail, Bull. Torrey Club 24: 305. 1897. Ceramanthus Malme, Ark. Bot. 414: 2. 1905. A few additional synonyms will have to be added from the South American flora. I am very reluctant to disregard Schlechter's separation of *Philibertia* and *Funastrum* (in Fedde, Repert. 13: 279-287. 1915), but feel that it is necessary to do so in order to maintain balance within the family. As far as I am aware, the only character really separating the two entities, upon the basis of present speciation, is the structure of the corolla, whether campanulate with shallow lobes in the former, or rotate with more deeply divided lobes in the latter. Other definitive structures apparently are lacking, and the striking similarity, if not identity, of the anther, pollinia, and corona characters is impressive. The high attachment of the corona bladders to the anthers, cited by Schlechter for Philibertia, manifestly does not hold. The annulus connecting the bladdery corona segments is usually more pronounced in Funastrum than in Philibertia, but is present in both. Sarcostemma, currently interpreted as including only Old World species, was erected by Robert Brown to include species now

WOODSON-NORTH AMERICAN ASCLEPIADACEAE. I 217

relegated to *Funastrum* and *Philibertia* as well. I can find no tangible distinction between the three, although they were placed in different subtribes by Schumann, as has been explained previously. Few North American species have been described since the prevalence of the restricted definition of *Sarcostemma*, and only the following transfers appear to be necessary:

SARCOSTEMMA **tomentella** (Brandg.) Woodson, comb. nov. *Philibertia tomentella* Brandg. Univ. Cal. Publ. Bot. **4**: 90. 1910.

- SARCOSTEMMA **Torreyi** (A.Gray) Woodson, comb. nov. *Philibertia Torreyi* A.Gray, Proc. Amer. Acad. **12**: 64. 1877.
 - Philibertella Torreyi (A.Gray) Vail, Bull. Torrey Club 24: 309. 1897.
 - Funastrum Torreyi (A.Gray) Schltr. in Fedde, Repert. 13: 287. 1915.

VI. MATELEA Aubl. Fl. Guian. 1: 277. t.109. 1775. Hostea Willd. Sp. Pl. 1: 1274. 1798.

Macroscepis HBK. Nov. Gen. 3: 200. 1819.
Pherotrichis Dene. Ann. Sci. Nat. Bot. ii. 9: 322. 1838.
Ibatia Dene. in DC. Prodr. 8: 599. 1844.
Polystemma Dene. loc. cit. 602. 1844.
Dictyanthus Dene. loc. cit. 604. 1844.
Chthamalia Dene. loc. cit. 605. 1844.
Ptycanthera Dene. loc. cit. 606. 1844.
Trichosacme Zucc. Abh. Akad. Wiss. München 4²: 11. 1845.
Tympananthe Hassk. Flora 30: 757. 1847.
Rytidoloma Turcz. Bull. Soc. Nat. Mosc. 25²: 319. 1852.
Callaeolepium Karst. Fl. Col. 2: 123. 1865.
Poicilla Griseb. Cat. Pl. Cub. 176. 1866.
Himantostemma A.Gray, Proc. Amer. Acad. 20: 294. 1885.
Rothrockia A.Gray, loc. cit. 295. 1885.

Tetracustelma Baill. Hist. Pl. 10: 292. 1891.
Urostephanus Robins. & Greenm. Amer. Journ. Sci. iii. 50: 159. 1895.

218ANNALS OF THE MISSOURI BOTANICAL GARDEN

Prosthecidiscus Donn.Sm. Bot. Gaz. 25: 149. 1898. Labidostelma Schltr. Bull. Herb. Boiss. ii. 6: 843. 1906. Microdactylon Brandg. Zoe 5: 252. 1908. Amphorella Brandg. Univ. Cal. Publ. Bot. 4: 91. 1910. Poicillopsis Schltr. in Urb. Symb. Ant. 7: 339. 1912. Pachystelma Brandg. Univ. Cal. Publ. Bot. 7: 330. 1920. Cyclodon Small, Man. Fl. 1075. 1933. Odontostephana Alexander, in Small, loc. cit. 1076. 1933. Edisonia Small, loc. cit. 1078. 1933. Heliostemma Woodson, Amer. Journ. Bot. 22: 689. 1935. Gonolobus and Vincetoxicum of North American authors, in large part.

To this imposing list of synonyms eventually will have to be added numerous generic names from the South American flora. Very few of these entities are strictly co-extensive, nearly all having been based upon some more or less striking variation of the corona. Loud protestations probably will be made by botanists familiar with such extremes as Dictyanthus and Macroscepis that at least those familiar genera should be allowed to stand inviolate, but I should like to lay a curse on the man who revives them without at least as much study as I have devoted. And I feel compelled to enjoin all future systematists to ponder long and deeply the intricacies of the gonoloboid corona before proposing additional novelties. The corona of Matelea, as is almost universal in the Cynanchoideae, consists of a unit enation of the anther filament, fundamentally subtending an additional enation (such as the hood and horn, respectively, of most species of Asclepias). The outer units may be separate, essentially entire, or with variously elaborated marginal lobules; at other times they may be concrescent into an inconspicuous, fimbriate skirt at the base of the gynostegium, into a ring, or into a massive rotate disc adnate to the corolla throat. The inner units may be small appendages of the anther head stipe rather high above the outer units, or may be combined, either essentially free or completely adnate, with the outer units. The result is a kaleidoscopic medley that can be conveyed in print only by the use of critical illustrations for each of the dozens of species.

219 WOODSON-NORTH AMERICAN ASCLEPIADACEAE. I

At one time during the studies which preceded this paper, an intensive study was made of the anther structure of the Gonoloboids, for I felt that the position of the anthers with respect to the stigma head (whether beneath or about the margin) would aid in the establishment of some of the favorite genera apparently doomed to synonymy. Here numerous trends were obvious, but nothing of sufficient stability for generic distinction. A long consideration of pollinium structure also was ended in rather bitter frustration. A peculiar vegetative character which links practically all the species groups of Matelea (although by no means every species of the groups) is the mixed indument consisting of long eglandular hairs and short, bulbose emergences. These emergences usually appear to be somewhat glandular, and may be white, dark brown, or black. Since no other group of Asclepiads with which I am familiar possesses such an indument, with the exception of the closely neighboring Fischeria maintained provisionally and with some misgivings, I regard its occurrence in Matelea as extremely significant. I am convinced that the elements which I have included in that genus are inextricably related. Heretofore, Matelea has been a genus of perhaps four South American species poorly represented in North American herbaria. Its expansion as advocated here consequently entails a shocking number of new combinations. Only a few of the generic synonyms (such as Macroscepis and Dictyanthus) contain as many as half a dozen species, however, and in view of that fact and the many nomenclatural changes necessary in any event it seems scarcely worth while to ask conservation for any of those names. Then, too, such a drastic reformation may better be served by a poorly known generic name than by one with more definitely established associations.

Recent tropical American collections are bringing to light more novelties in Matelea than perhaps in any other genus of Asclepiads. Therefore I have prepared the following key to subgenera and sections, both to illustrate the reformation of the genus and as a temporary aid to herbarium study. I have treated several groups as subgenera simply because they have

220 ANNALS OF THE MISSOURI BOTANICAL GARDEN

familiar names and in spite of the fact that their characters are less important than certain others which are treated as sections, having no previous generic name (for I am wary of treating them as nouns lest some floristic student raise them to genera). As accumulation of Asclepiads from tropical North America proceeds, additional entries will have to be inserted in the key. That should accentuate the greater convenience of an ultra-conservative generic concept. As a final word, it should be emphasized that the species groups show great variation amongst their constituents, and that they cannot safely be raised to generic rank as they now exist. Certain species show affinities for more than one group. Where I have made an arbitrary disposition in such cases I usually have included notes or references to aid their identification.

KEY TO THE SUBGENERA AND SECTIONS

A. Pollinia more or less descending from the translator arms.

B. Corolla subcampanulate-rotate, without a faucal annulus, the limb merely continuing the dilation of the throat and much longer than it; corona annular, the 5 constituent segments usually distinctly 3-lobed; pollinia frequently prolonged beyond the attachment of BB. Corolla very broadly campanulate, the lobes very broad and scarcely as long as the shallow open throat, without a faucal annulus; corona rotate, of 5 segments consisting of 2 falcate outer lobes and a median inflexed lobule; pollinia conspicuously excavated on both BBB. Corolla salverform-rotate, usually with a faucal annulus, the limb abruptly spreading or somewhat reflexed from the short tube. C. Corolla lobes without caudate appendages; corona of 5 digitate segments adnate to the corolla tube, each with a more or less distinct callous boss supporting the stigma head; pollinia without apical processes; plants variously pubescent, but not white-woolly CC. Corolla lobes with long plumose caudate appendages; corona annular, shallowly 5-lobed, each lobe with an inconspicuous internal ligule; pollinia with a slender apical process; entire plant very

- AA. Pollinia essentially horizontal, but occasionally arcuate, with the tips somewhat ascending or descending.
 - B. Antillean species (corolla rotate; if deeply campanulate, see Pachystelma).

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WOODSON-NORTH AMERICAN ASCLEPIADACEAE. I 221

D. Erect or prostrate herbs; corolla lobes ascending.

DD. Lianas or twining undershrubs (except M. caudata); corolla lobes reflexed or spreading.

E. Corolla without a faucal annulus exterior to the true corona.

tions superposed.

222

ANNALS OF THE MISSOURI BOTANICAL GARDEN

- EE. Corona segments simply digitate or merely somewhat carunculate, adnate to the corolla throat at least at the base; corolla lobes essentially glabrous within.

SUBGENUS 1. IBATIA

MATELEA araneosus (Donn.Sm.) Woodson, comb. nov. Gonolobus araneosus Donn.Sm. Bot. Gaz. 47: 257. 1909.
MATELEA atrocoronata (Brandg.) Woodson, comb. nov. Vincetoxicum atrocoronatum Brandg. Univ. Cal. Publ. Bot. 6: 372. 1917.
MATELEA chrysantha (Greenm.) Woodson, comb. nov. Gonolobus chrysanthus Greenm. Proc. Amer. Acad. 32: 299. 1897.

Vincetoxicum chrysanthum (Greenm.) Standl. Contr. U.S. Nat. Herb. 23: 1190. 1924. MATELEA cordifolia (A.Gray) Woodson, comb. nov.

Rothrockia cordifolia A.Gray, Proc. Amer. Acad. 20: 295. 1885.

MATELEA fruticosa (Brandg.) Woodson, comb. nov.
Rothrockia fruticosa Brandg. Zoe 5: 165. 1903.
MATELEA gonoloboides (Robins. & Greenm.) Woodson, comb. nov.

Urostephanus gonoloboides Robins. & Greenm. Amer. Journ. Sci. iii. 50: 159. 1895.

MATELEA inconspicua (Brandg.) Woodson, comb. nov. Gonolobus inconspicuus Brandg. Univ. Cal. Publ. Bot. 3: 387. 1909.

MATELEA maritima (Jacq.) Woodson, comb. nov.

Cynanchum maritimum Jacq. Stirp. Amer. 83. pl.56. 1763.

Gonolobus maritimus (Jacq.) R.Br. Mem. Wern. Soc. 1:

35. 1809.

Gonolobus floccosus Bertol. Opusc. 4: 521. 1823. Gonolobus suberosus Spreng. Syst. 1: 846. 1825, non R.Br.

WOODSON-NORTH AMERICAN ASCLEPIADACEAE. I 223

Ibatia maritima (Jacq.) Dcne. in DC. Prodr. 8: 599. 1844. Lachnostoma maritimum (Jacq.) Nichols. Dict. Gard. 2: 236. 1884. Ibatia muricata Griseb. Fl. B.W.I. 421. 1861. MATELEA mollis (Griseb.) Woodson, comb. nov. Ibatia mollis Griseb. Cat. Pl. Cub. 177. 1866. Lachnostoma molle (Griseb.) Maza, Cat. Periant. 276.

1894.

Ptychanthera mollis (Griseb.) Schltr. in Urb. Symb. Ant. 1: 280. 1899.

MATELEA patalensis (Donn.Sm.) Woodson, comb. nov. Gonolobus patalensis Donn.Sm. Bot. Gaz. 47: 256. 1909.
MATELEA petiolaris (A.Gray) Woodson, comb. nov. Gonolobus petiolaris A.Gray, Proc. Amer. Acad. 21: 397. 1886.

Vincetoxicum petiolare (A.Gray) Standl. Contr. U.S. Nat. Herb. 23: 1189. 1924.

MATELEA porphyrantha (Standl.) Woodson, comb. nov.
Vincetoxicum porphyranthum Standl. ex Yuncker, Field
Mus. Publ. Bot. 17: 387. 1938.
MATELEA Pringlei (A.Gray) Woodson, comb. nov.

Himantostemma Pringlei A.Gray, Proc. Amer. Acad. 20: 294. 1885.

MATELEA Prosthecidiscus Woodson, nom. nov.

Prosthecidiscus guatemalensis Donn.Sm. Bot. Gaz. 25: 150. pl.12. 1898, non Matelea guatemalensis (K.Sch.) Woodson.

MATELEA pueblensis (Brandg.) Woodson, comb. nov. Vincetoxicum pueblensis Brandg. Univ. Cal. Publ. Bot. 4: 91. 1910.

MATELEA Purpusii (Brandg.) Woodson, comb. nov. Gonolobus Purpusii Brandg. Univ. Calif. Publ. Bot. 3: 387. 1909.

MATELEA tristiflora (Standl.) Woodson, comb. nov. Vincetoxicum tristiflorum Standl. Field Mus. Publ. Bot.

17: 272. 1937.
 MATELEA umbellata (Brandg.) Woodson, comb. nov.
 Rothrockia umbellata Brandg. Zoe 5: 165. 1903.

224 ANNALS OF THE MISSOURI BOTANICAL GARDEN

MATELEA Warscewiczii (Karst.) Woodson, comb. nov. Callaeolepium Warscewiczii Karst. Fl. Col. 2: 123. pl. 165. 1865. Fimbristemma Warscewiczii (Karst.) Bonth & Hook

Fimbristemma Warscewiczii (Karst.) Benth. & Hook. Gen. Pl. 2: 768. 1876.

Ibatia is placed in the key as having "pendulous" pollinia since their vertical dimension is at least equal to the horizontal and usually is greater. Some confusion with *Chthamalia* is likely to occur, but may be avoided by a comparison of the coronas, that of the former subgenus being without internal ligules or bosses adnate to the segments and that of the latter always having such structures.

SUBGENUS 2. LABIDOSTELMA

MATELEA Quirosii (Standl.) Woodson, comb. nov. Cynanchum rotatum Sesse & Mociño, Fl. Mex. 76. 1887, non Vell.

Labidostelma guatemalense Schltr. Bull. Herb. Boiss. ii.
6: 843. 1906, non M. guatemalensis (Donn.Sm.) Woodson.

Vincetoxicum Quirosii Standl. Field Mus. Publ. Bot. 183:

959. 1938.

SUBGENUS 3. MACROSCEPIS

MATELEA calcicola (Greenm.) Woodson, comb. nov.

Gonolobus calcicola Greenm. Proc. Amer. Acad. 40: 30. 1904.

Vincetoxicum calcicola (Greenm.) Standl. Contr. U.S. Nat. Herb. 23: 1191. 1924.

MATELEA congesta (Dene.) Woodson, comb. nov.
Gonolobus congestus Dene. in DC. Prodr. 8: 597. 1844.
Vincetoxicum congestum (Dene.) Standl. Contr. U.S. Nat.

Herb. 23: 1189. 1924.

MATELEA congestiflora (Donn.Sm.) Woodson, comb. nov. Cynanchum hirsutum Sesse & Mociño, Fl. Mex. 76. 1887,

- non Vell.
- Macroscepis congestiflora Donn.Sm. Bot. Gaz. 25: 149. 1898.

225 WOODSON-NORTH AMERICAN ASCLEPIADACEAE, I

MATELEA diademata (Edwards) Woodson, comb. nov. Gonolobus diadematus Edwards, Bot. Reg. 3: pl.252. 1817.

- Vincetoxicum diadematum (Edwards) Standl. Contr. U.S. Nat. Herb. 23: 1188. 1924.
- MATELEA magnifolia (Pittier) Woodson, comb. nov. Gonolobus magnifolius Pittier, Contr. U.S. Nat. Herb. 13:

104. fig.13. 1910. Vincetoxicum magnifolium (Pittier) Standl. loc. cit. 23: 1188. 1924. MATELEA obovata (HBK.) Woodson, comb. nov. Macroscepis obovata HBK. Nov. Gen. 3: 200. 1819. SUBGENUS 4. TRICHOSACME MATELEA lanata (Zucc.) Woodson, comb. nov. Trichosacme lanata Zucc. Abh. Akad. Wiss. Munchen 42: 11. 1845.

An explanation, if not an apology, is in order for reducing Trichosacme from generic status. M. lanata is quite unmistakable because of the copius lanate pubescence and long plumose corolla lobes; but aside from these particulars it is manifestly intermediate between other groups, having somewhat the corona of Chthamalia, the pollinia of Ibatia, and the corolla (except the lobe appendages) of a miniature Macroscepis.

SUBGENUS 5. POICILLA

MATELEA ovatifolia (Griseb.) Woodson, comb. nov. Poicilla ovatifolia Griseb. Cat. Pl. Cub. 177. 1866. Ptychanthera ovatifolia (Griseb.) Schltr. in Urb. Symb. Ant. 1: 279. 1899. MATELEA tamnifolia (Griseb.) Woodson, comb. nov. Poicilla tamnifolia Griseb. Cat. Pl. Cub. 176. 1866.

SUBGENUS 6. PTYCANTHERA

§. Pauciflorae

MATELEA acuminata (Griseb.) Woodson, comb. nov. Orthosia acuminata Griseb. Cat. Pl. Cub. 175. 1866. Ptychanthera Berterii acc. to Schltr. in Urb. Symb. Ant. 1: 279. 1899, non Dcne.

ANNALS OF THE MISSOURI BOTANICAL GARDEN

- Poicilla acuminata (Griseb.) Schltr. loc. cit. 5: 469. 1908.
- Poicillopsis acuminata (Griseb.) Schltr. loc. cit. 7: 339. 1912.
- MATELEA nipensis (Urb.) Woodson, comb. nov. Gonolobus nipensis Urb. Symb. Ant. 9: 421. 1925. MATELEA oblongata (Griseb.) Woodson, comb. nov.

Orthosia oblongata Griseb. Cat. Pl. Cub. 176. 1866. Ptychanthera oblongata (Griseb.) Schltr. in Urb. Symb. Ant. 1: 280. 1899.

Poicilla oblongata (Griseb.) Schltr. loc. cit. 5: 470. 1908.

Poicillopsis oblongata (Griseb.) Schltr. loc. cit. 7: 339. 1912.

MATELEA pauciflora (Spreng.) Woodson, comb. nov. Gonolobus pauciflorus Spreng. Syst. 1: 846. 1825. Ptycanthera Berterii Dcne. in DC. Prodr. 8: 606. 1844, not acc. to Schltr. in Urb. Symb. Ant. 1: 279. 1899.

§. Variifoliae

226

MATELEA bayatensis (Urb.) Woodson, comb. nov.

Gonolobus bayatensis Urb. Symb. Ant. 9: 420. 1925. MATELEA Ekmanii (Urb.) Woodson, comb. nov. Gonolobus Ekmanii Urb. Symb. Ant. 9: 422. 1925. MATELEA Sintenisii (Schltr.) Woodson, comb. nov. Gonolobus Sintenisii Schltr. in Urb. Symb. Ant. 1: 288. 1899.

Vincetoxicum Sintenisii (Schltr.) Britton, Sci. Surv. Porto Rico & Virgin Isl. 6: 100. 1925. MATELEA tigrina (Griseb.) Woodson, comb. nov. Gonolobus tigrinus Griseb. Pl. Wright. 520. 1862. MATELEA variifolia (Schltr.) Woodson, comb. nov. Gonolobus variifolius Schltr. in Urb. Symb. Ant. 1: 286. 1899.

Vincetoxicum variifolium (Schltr.) Britton, Sci. Surv. Porto Rico & Virgin Isl. 6: 100. 1925.

The subgenus Ptycanthera was largely the deciding factor in the inclusive treatment of Matelea which I have adopted.

WOODSON-NORTH AMERICAN ASCLEPIADACEAE. I 227

Were it not for the Antillean species, one might compose a fairly respectable key to several genera upon the continent, following generally the lines of the key to subgenera and sections of Matelea as it now appears. However, the Antillean species cut so sharply across most of the distinctions between the continental groups that the only way I can distinguish them from the latter in print is by the geographical factor. Were it not for their ambiguity with respect to the continental entities, one might obliterate Ptycanthera entirely, distributing §. Pauciflorae and §. Variifoliae, perhaps, to the continental subgenera Eumatelea and Heliostemma respectively. Variation of the corona in *Ptycanthera* appears largely to be responsive to the development of the anther head stipe. Where the latter is fairly pronounced, in § Pauciflorae, the corona adopts much the same fluted appearance with subtending skirt as in Eumatelea § Reticulatae; but where the anther head is sessile (§ Variifoliae), the corona becomes a rotate disc as in Heliostemma, or a shallow 5-angled ring, in either case with 5 partitions, bosses, or hooks corresponding to the fluted buttresses of § Pauciflorae. In M. Sintenisii the compression of the anther head and corona apparently has led to the formation by the corolla throat of a rather prominent faucal annulus. The anther and pollinium structures are somewhat more variable even than in the continental species. Yet, withal, the superficial aspect of the various species is so similar in most cases that I cannot but view them as extremely closely related, particularly in view of their restricted geographical distribution. The exasperations attendant upon their attempted segregation are illustrated graphically by Schlechter's vacillation between Poicilla, Ptycanthera (spelled Ptychanthera by him), Poicillopsis, and Gonolobus, with the familiar Vincetoxicum-motif supplied by Dr. Britton.

SUBGENUS 7. CHTHAMALIA

MATELEA adenocardium (Standl.) Woodson, comb. nov.
Vincetoxicum adenocardium Standl. Field Mus. Publ. Bot.
17: 267. 1937.
MATELEA Baldwyniana (Sweet) Woodson, comb. nov.

228ANNALS OF THE MISSOURI BOTANICAL GARDEN

Gonolobus Baldwynianus Sweet, Hort. Brit. ed.2. 360. 1830.

Vincetoxicum Baldwinianum (Sweet) Britton, Mem. Torrey Club 5: 265. 1894.

Odontostephana Baldwiniana (Sweet) Alexander, in Small, Man. Fl. 1077. 1933.

MATELEA biflora (Raf.) Woodson, comb. nov.

Gonolobus biflorus Raf. New Fl. N. Amer. 4: 58. 1836. Chthamalia biflora (Raf.) Dene. in DC. Prodr. 8: 605. 1844.

- Vincetoxicum biflorum (Raf.) Heller, Contr. Herb. Franklin & Marshall Coll. 1: 79. 1895.
- MATELEA brevicoronata (Robins.) Woodson, comb. nov. Gonolobus parviflorus var. brevicoronatus Robins. Proc. Amer. Acad. 26: 169. 1891.
- MATELEA camporum (Brandg.) Woodson, comb. nov. Vincetoxicum camporum Brandg. Univ. Calif. Publ. Bot. 4: 185. 1911.
- MATELEA carolinensis (Jacq.) Woodson, comb. nov. Cynanchum carolinense Jacq. Coll. 2: 288. 1788. Gonolobus carolinensis (Jacq.) R.Br. Mem. Wern. Soc. 1:

 $35.\ 1809.$

Vincetoxicum carolinense (Jacq.) Britton, Mem. Torrey Club 5: 265. 1894.

Odontostephana carolinensis (Jacq.) Alexander, in Small, Man. Fl. 1077. 1933.

MATELEA cynanchoides (Engelm.) Woodson, comb. nov. Gonolobus cynanchoides Engelm. in Engelm. & Gray, Boston Journ. Nat. Hist. 5: 251. 1845.

Vincetoxicum cynanchoides (Engelm.) Heller, Muhlenbergia 1: 2. 1900.

MATELEA decipiens (Alexander) Woodson, comb. nov. Odontostephana decipiens Alexander, in Small, Man. Fl. 1077. 1933.

Gonolobus decipiens (Alexander) Perry, Rhodora 40: 286. 1938.

MATELEA flavidula (Chapm.) Woodson, comb. nov. Gonolobus flavidulus Chapm. Bot. Gaz. 3: 12. 1878.

WOODSON-NORTH AMERICAN ASCLEPIADACEAE. I 229

Gonolobus hirsutus var. flavidulus (Chapm.) A.Gray, Syn. Fl. ed.2, 2¹: 404. 1886.
Vincetoxicum flavidulum (Chapm.) Heller, Muhlenbergia 1: 2. 1900.
Odontostephana flavidula (Chapm.) Alexander, in Small, Man. Fl. 1078. 1933.
MATELEA floridana (Vail) Woodson, comb. nov.
Vincetoxicum floridanum Vail, Bull. Torrey Club 26: 428. 1899.

Odontostephana floridana (Vail) Alexander, in Small, Man. Fl. 1078. 1933.

MATELEA Greggii (Vail) Woodson, comb. nov.

Vincetoxicum Greggii Vail, Bull. Torrey Club 26: 431. 1899.

MATELEA LeSueurii (Standl.) Woodson, comb. nov. Vincetoxicum LeSueurii Standl. Field Mus. Publ. Bot. 17: 270, 1937.

The pollinia of this species are not the subquadrate-reniform sort typical of *Chthamalia*, but are more nearly triangularpyriform. Nevertheless, the affinities of *M. LeSueurii* unmistakably are with that subgenus, particularly with *M. Nummularia*.

- MATELEA Nummularia (Dcne.) Woodson, comb. nov. Chthamalia Nummularia Dcne. in DC. Prodr. 8: 605. 1844.
- MATELEA obliqua (Jacq.) Woodson, comb. nov.
 Cynanchum obliquum Jacq. Coll. 1: 148. 1786.
 Gonolobus obliquus (Jacq.) R.Br. Mem. Wern. Soc. 1: 35. 1809.
 - Vincetoxicum obliquum (Jacq.) Britton, Mem. Torrey Club 5: 266. 1894.
 - Odontostephana obliqua (Jacq.) Alexander, in Small, Man. Fl. 1077. 1933.
- MATELEA parviflora (Torr.) Woodson, comb. nov.

Lachnostoma (?) parviflorum Torr. Rept. Bot. Mex. Bound. Surv. 165. 1859.
Gonolobus parviflorus (Torr.) A.Gray, Proc. Amer. Acad.
12: 79. 1877.

230 ANNALS OF THE MISSOURI BOTANICAL GARDEN

Vincetoxicum parviflorum (Torr.) Heller, Muhlenbergia
1: 2. 1900.
MATELEA parvifolia (Torr.) Woodson, comb. nov.
Gonolobus parvifolius Torr. Rept. Bot. Mex. Bound. Surv.
166. 1859.
Gonolobus hastulatus A.Gray, Proc. Amer. Acad. 12: 78.
1877.

Vincetoxicum hastulatum (A.Gray) Heller, Muhlenbergia 1: 2. 1900.

Gonolobus californicus Jepson, Man. 771. 1925.
MATELEA pedunculata (Dcne.) Woodson, comb. nov.
Chthamalia pedunculata Dcne. in DC. Prodr. 8: 605. 1844.
MATELEA producta (Torr.) Woodson, comb. nov.
Gonolobus productus Torr. Rept. Bot. Mex. Bound. Surv.
165. 1859.

Vincetoxicum productum (Torr.) Vail, Bull. Torrey Club 26: 431. 1899.

MATELEA prostrata (Willd.) Woodson, comb. nov.

Cynanchum prostratum Willd. Sp. Pl. 1: 1257. 1798. Gonolobus prostratus (Willd.) R.Br. Mem. Wern. Soc. 1: 35. 1809.

Lachnostoma prostratum (Willd.) Dene. in DC. Prodr. 8: 602. 1844.

Tetracustelma prostrata (Willd.) Baill. Hist. Pl. 10: 292. 1891.

MATELEA pubiflora (Dcne.) Woodson, comb. nov.
Chthamalia pubiflora Dcne. in DC. Prodr. 8: 605. 1844.
Gonolobus pubiflorus (Dcne.) Engelm. in Engelm. & Gray, Boston Journ. Nat. Hist. 5: 252. 1845.
Vincetoxicum pubiflorum (Dcne.) Heller, Muhlenbergia 1: 2. 1900.

Edisonia pubiflora (Dcne.) Small, Man. Fl. 1078. 1933. MATELEA Schaffneri (A.Gray) Woodson, comb. nov. Gonolobus Schaffneri A.Gray, in Hemsl. Biol. Centr.-Am.

- Bot. 2: 334. 1882; A.Gray, Proc. Amer. Acad. 21: 399. 1886.
- Gonolobus bifidus Hemsl. Biol. Centr.-Amer. Bot. 2: 330. 1882.

231 WOODSON-NORTH AMERICAN ASCLEPIADACEAE. I

MATELEA Shortii (A.Gray) Woodson, comb. nov. Gonolobus obliquus var. Shortii A.Gray, Syn. Fl. 21: 104. 1878.

Vincetoxicum Shortii (A.Gray) Britton, Mem. Torrey Club 5: 266. 1894.

Gonolobus Shortii A.Gray, Bot. Gaz. 8: 191. 1883. Odontostephana Shortii (A.Gray) Alexander, in Small,

Man. Fl. 1077. 1933. MATELEA stenopetala (A.Gray) Woodson, comb. nov. Gonolobus stenopetalus A.Gray, Proc. Amer. Acad. 21: 398. 1886. Vincetoxicum stenopetalum (A.Gray) Standl. Contr. U.S. Nat. Herb. 23: 1190. 1924. MATELEA Vailiana Woodson, nom. nov. Gonolobus acuminatus A.Gray, Proc. Amer. Acad. 21: 399. 1886, non Matelea acuminata (Griseb.) Woodson. Vincetoxicum acuminatum (A.Gray) Vail, Bull. Torrey Club 26: 431. 1899. MATELEA Wootonii (Vail) Woodson, comb. nov. Vincetoxicum Wootonii Vail, Bull. Torrey Club 28: 485. pl.30. 1901.

This is the characteristic group of Matelea in northern Mexico and the southern United States. The pollinia are well illustrated for the species "in the Manual Range" by Miss Perry (Rhodora 40: pl.494. 1938) where the contrasting features of true Gonolobus pollinia are shown also. I believe that Chthamalia is perhaps most closely related to Ibatia amongst the subgenera of Matelea, the "pendulous" pollinia of the latter frequently appearing much like the "horizontal" pollinia of the former (merely of greater vertical dimension). The corona of the two subgenera, also, are much alike, but the internal ligules of the former are merely adnate (sometimes nearly free) to the outer segments, whereas the fusion is virtually complete in the latter.

SUBGENUS 8. PHEROTRICHIS MATELEA Balbisii (Dcne.) Woodson, comb. nov.

232 ANNALS OF THE MISSOURI BOTANICAL GARDEN

Asclepias villosa Balb. Mem. Accad. Sci. Torino 7: 386. 1803, non Mill.

Cynanchum villosum (Balb.) R. & S. Syst. 6: 103. 1819.
Lachnostoma Balbisii Dene. in DC. Prodr. 8: 602. 1844.
Gonolobus pogonanthus Hemsl. Biol. Centr.-Am. Bot. 2: 333. 1882.

Pherotrichis Balbisii (Dcne.) A.Gray, Proc. Amer. Acad.

21: 400. 1886; Syn. Fl. ed.2. 2¹: 462. 1886. Pherotrichis Schaffneri A.Gray, loc. cit. 1886.
MATELEA chihuahuensis (A.Gray) Woodson, comb. nov. Gonolobus chihuahuensis A.Gray, Proc. Amer. Acad. 21: 398. 1886.
Vincetoxicum chihuahuense (A.Gray) Standl. Field Mus. Publ. Bot. 17: 270. 1937.
MATELEA leptogenia (Robins.) Woodson, comb. nov. Pherotrichis leptogenia Robins. Proc. Amer. Acad. 29: 319. 1894.

SUBGENUS 9. AMPHORELLA

MATELEA castanea (Brandg.) Woodson, comb. nov. Amphorella castanea Brandg. Univ. Calif. Publ. Bot. 4:

92. 1910.

SUBGENUS 10. TIARASTEMMA

MATELEA calcarata Woodson, comb. nov.

Vincetoxicum calcaratum Woodson, Amer. Journ. Bot. 22: 689. pl.1. fig.8. 1935.

MATELEA belizensis (Lundell & Standl.) Woodson, comb. nov. Vincetoxicum belizense Lundell & Standl. in Standl. Field Mus. Publ. Bot. 17: 268. 1937.

SUBGENUS 11. POLYSTEMMA

MATELEA Decaisnei Woodson, nom. nov.

Polystemma viridiflora Dene. in DC. Prodr. 8: 602. 1844, non M. viridiflora (G.F.W.Mey.) Woodson.
MATELEA rupestris (Brandg.) Woodson, comb. nov.
Polystemma rupestre Brandg. Univ. Cal. Publ. Bot. 7: 330. 1920.

MATELEA scopulorum (Brandg.) Woodson, comb. nov.

WOODSON-NORTH AMERICAN ASCLEPIADACEAE. I 233

Polystemma scopulorum Brandg. Univ. Calif. Publ. Bot.6: 189. 1915.

SUBGENUS 12. HELIOSTEMMA

MATELEA caudata (A.Gray) Woodson, comb. nov. Gonolobus caudatus A.Gray, Proc. Amer. Acad. 21: 399. 1886.

Vincetoxicum caudatum (A.Gray) Standl. Contr. U.S.

Nat. Herb. 23: 1190. 1924. MATELEA crenata (Vail) Woodson, comb. nov. Vincetoxicum crenatum Vail, Bull. Torrey Club 26: 429. 1899.

This species might almost as well be placed in *Ibatia* upon the basis of the pollinia alone, for they are only slightly falciform. The corona segments, also, are scarcely typical of *Heliostemma* in that they are not strongly adnate to the corolla throat. However, they do have a conspicuous internal boss which is characteristic of the latter subgenus and never found in the former.

MATELEA cyclophylla (Standl.) Woodson, comb. nov.
Vincetoxicum cyclophyllum Standl. Contr. U.S. Nat. Herb.
23: 1191. 1924.

MATELEA nigrescens (Schlecht.) Woodson, comb. nov.
Gonolobus nigrescens Schlecht. Linnaea 8: 522. 1833.
Vincetoxicum nigrescens (Schlecht.) Standl. Contr. U.S.
Nat. Herb. 23: 1192. 1924.
MATELEA picturata (Hemsl.) Woodson, comb. nov.

Gonolobus picturatus Hemsl. Biol. Centr.-Am. Bot. 2: 332. 1882.

MATELEA pilosa (Benth.) Woodson, comb. nov. Gonolobus pilosus Benth. Pl. Hartw. 289. 1848. Gonolobus atratus A.Gray, Proc. Amer. Acad. 22: 436. 1887.

Gonolobus suberiferus Robins. Proc. Amer. Acad. 27:

181. 1892. *Vincetoxicum Grayanum* Standl. Contr. U.S. Nat. Herb.
23: 1191. 1924.

234ANNALS OF THE MISSOURI BOTANICAL GARDEN

Vincetoxicum pilosum (Benth.) Standl. loc. cit. 1924. Vincetoxicum suberiferum (Robins.) Standl. loc. cit. 1189. 1924.

Vincetoxicum quercetorum Standl. Field Mus. Publ. Bot. 17: 271. 1937.

MATELEA Pittieri (Standl.) Woodson, comb. nov. Vincetoxicum Pittieri Standl. Field Mus. Publ. Bot. 17: 270. 1937. Vincetoxicum discolor Woodson, Ann. Missouri Bot. Gard. 25: 833. fig.1. 1938. SUBGENUS 13. EUMATELEA §. Reticulatae MATELEA alabamensis (Vail) Woodson, comb. nov. Vincetoxicum alabamense Vail, Bull. Torrey Club 30: 178. pl.9. 1903. MATELEA campechiana (Standl.) Woodson, comb. nov. Vincetoxicum campechianum Standl. Carnegie Inst. Wash. Publ. 461: 82. 1935. MATELEA Gentlei (Lundell & Standl.) Woodson, comb. nov. Vincetoxicum Gentlei Lundell & Standl. Field Mus. Publ. Bot. 17: 269. 1937. MATELEA lanceolata (Dcne.) Woodson, comb. nov. Gonolobus lanceolatus Dene. in DC. Prodr. 8: 598. 1844. Vincetoxicum stenophyllum Standl. Contr. U.S. Nat. Herb. 23: 1188. 1924. MATELEA reticulata (Engelm.) Woodson, comb. nov. Gonolobus reticulatus Engelm. ex A.Gray, Proc. Amer. Acad. 12: 75. 1877. Vincetoxicum reticulatum (Engelm.) Heller, Bot. Expl. Texas, 79. 1895. MATELEA Tuerckheimii (Donn.Sm.) Woodson, comb. nov. Gonolobus Tuerckheimii Donn. Sm. Bot. Gaz. 44: 116. 1907.

Vincetoxicum trichoneuron Standl. ex Yuncker, Field

Mus. Publ. Bot. 17: 388. 1938. MATELEA velutina (Schlecht.) Woodson, comb. nov. Gonolobus velutinus Schlecht. Linnaea 8: 521. 1833.

WOODSON-NORTH AMERICAN ASCLEPIADACEAE. I 235

Vincetoxicum velutinum (Schlecht.) Standl. Contr. U.S. Nat. Herb. 23: 1189. 1924.

§. Pseudobarbatae

MATELEA guatemalensis (K.Sch.) Woodson, comb. nov.
Gonolobus velutinus var. calycinus Donn.Sm. Bot. Gaz.
13: 189. 1888.

Gonolobus guatemalensis K.Sch. in Engl. & Prantl, Nat.

Pflanzenfam. 4²: 302. 1895.
MATELEA pinguifolia (Standl.) Woodson, comb. nov.
Vincetoxicum pinguifolium Standl. Journ. Wash. Acad.
Sci. 17: 13. 1927.
MATELEA pseudobarbata (Pittier) Woodson, comb. nov.
Gonolobus pseudobarbatus Pittier, Contr. U.S. Nat.
Herb. 13: 105. fig.14. 1910.

Matelea nigrescens shows a strong affinity with this section, but has been placed in *Heliostemma* because of its falciform pollinia.

§. Viridiflorae
 MATELEA grandiflora (Standl.) Woodson, comb. nov.
 Vincetoxicum grandiflorum Standl. Carnegie Inst.
 Wash. Publ. 461: 83. 1935.

MATELEA viridiflora (G.F.W.Mey.) Woodson, comb. nov. Cynanchum viridiflorum G.F.W.Mey. Prim. Fl. Esseq. 141. 1818.

Gonolobus viridiflorus (G.F.W.Mey.) R. & S. Syst. 6: 61. 1819.

Vincetoxicum viridiflorum (G.F.W.Mey.) Standl. Contr. U.S. Nat. Herb. 27: 311. 1928.

This little group illustrates the maddening complications that result from attempts at segregation in the Gonolobeae. *M. viridiflora* and *M. grandiflora* quite obviously are very closely related, as evidenced particularly by the interrupted corolline annulus. Other characters, however, point strongly to relationship with other groups of *Matelea*, with the exception of the pollinia, which are scarcely similar to those of *Eumatelea*, and can be construed as "triangular-pyriform"

236ANNALS OF THE MISSOURI BOTANICAL GARDEN

only with a considerable stretch of the imagination. But on the other hand, the pollinia of the two species are so dissimilar that I can find no descriptive term to cover both, and at the same time to distinguish them from Eumatelea.

SUBGENUS 14. MICRODACTYLON

MATELEA cordata (Brandg.) Woodson, comb. nov. Microdactylon cordatum Brandg. Zoe 5: 252. 1908.

SUBGENUS 15. PACHYSTELMA

MATELEA bicolor (Britton & Wilson) Woodson, comb. nov. Marsdenia bicolor Britton & Wilson, Bull. Torrey Club 50: 47. 1923.

Gonolobus bicolor (Britton & Wilson) Urb. Symb. Ant. 9: 421. 1925.

MATELEA crassifolia (Standl.) Woodson, comb. nov. Vincetoxicum crassifolium Standl. Field Mus. Publ. Bot. **8**: 36. 1930.

MATELEA megacarpha (Brandg.) Woodson, comb. nov. Vincetoxicum megacarphum Brandg. Univ. Cal. Publ. Bot. 4: 381. 1913.

Pachystelma cordatum Brandg. loc. cit. 7: 330. 1920. Dictyanthus brachistanthus Standl. Field Mus. Publ. Bot. **8**: 38. 1930.

SUBGENUS 16. DICTYANTHUS

MATELEA altatensis (Brandg.) Woodson, comb. nov. Gonolobus altatensis Brandg. Zoe 5: 244. 1908. MATELEA ceratopetala (Donn.Sm.) Woodson, comb. nov. Dictyanthus ceratopetalus Donn.Sm. Bot. Gaz. 18: 208. 1893.

MATELEA dictyantha Woodson, nom. nov.

Rytidoloma reticulata Turcz. Bull. Soc. Nat. Mosc. 252: 320. 1852, non Matelea reticulata (Engelm.) Woodson. Dictyanthus reticulatus (Turcz.) Benth. & Hook. Gen. Pl. **2**: 765. 1876.

MATELEA diffusa Woodson, nom. nov. Dictyanthus prostratus Brandg. Univ. Cal. Publ. Bot. 7: 329. 1920, non Matelea prostrata (Willd.) Woodson.

237 WOODSON-NORTH AMERICAN ASCLEPIADACEAE. I

MATELEA Hemsleyana Woodson, nom. nov. Dictyanthus parviflorus Hemsl. Biol. Centr. Am. Bot. 2: 329. 1882, non Matelea parviflora (Torr.) Woodson. MATELEA Pavonii (Dcne.) Woodson, comb. nov. Dictyanthus Pavonii Dcne. in DC. Prodr. 8: 605. 1844. Tympananthe suberosa Hassk. Flora 30: 758. 1847. MATELEA Standleyana Woodson, nom. nov. Dictyanthus tigrinus Conzatti & Standl. in Standl. Contr. U.S. Nat. Herb. 23: 1183. 1924, non Matelea tigrina (Griseb.) Woodson. MATELEA stapeliaeflora (Reichb.) Woodson, comb. nov. Dictyanthus stapeliaeflora Reichb. Sel. Sem. Hort. Dresden, 4. 1850. MATELEA tuberosa (Robins.) Woodson, comb. nov. Dictyanthus tuberosus Robins. Proc. Amer. Acad. 27: 180. 1892. MATELEA yucatanensis (Standl.) Woodson, comb. nov. Dictyanthus yucatanensis Standl. Field Mus. Publ. Bot. 8: 37. 1930.

Dictyanthus aeneus Woodson, Amer. Journ. Bot. 22: 691. 1935.

I am very reluctant to merge Dictyanthus with Matelea, since the various species here show considerably more coherence and distinction than in other generic groups. However, generic lines cannot be drawn sharply due to such groups as Pachystelma, Labidostelma, and Macroscepis. The only really unique feature of *Dictyanthus* is that the faucal callus, or annulus, of the corolla is digitate, as are the segments of the corona. I am prepared for vigorous opposition from those who are accustomed to think of *Dictyanthus* as exemplified by D. Pavonii. M. altatensis provides a very suggestive link with either Pachystelma or Eumatelea, according to one's viewpoint at a particular time.

VII. FISCHERIA DC. Cat. Hort. Monsp. 112. 1813. I am maintaining Fischeria with misgivings, and only pro-

visionally, since its affinities with the broad interpretation of

238 ANNALS OF THE MISSOURI BOTANICAL GARDEN

Matelea are unmistakable, as shown particularly in the pollinium structure and the mixed indument with interspersed bulbose, glandular hairs. In the Central American species the corona appears outstanding, but is scarcely different from that of Eumatelea § Pseudobarbatae. The anthers, also, show the inflated vesicular development mentioned in the key to genera. But in F. viridis Moldenke, recently discovered in Colombia, the corona is resolved into a more typical structure for Matelea, and the anthers are not vesicular. Should more species comparable to F. viridis appear in the rich South American flora, it is difficult to foresee what characters could be found to support the genus other than the crisped corolla lobes. Since Fischeria is not well represented in North America, the species there being quite easily distinguished, I am leaving the question of its validity until I am more familiar with the South American congeners.

VIII. GONOLOBUS Michx. Fl. Bor. Am. 1: 119. 1803. Vincetoxicum Walt. Fl. Carol. 13, 104. 1788, non Moench. Fimbristemma Turcz. Bull. Soc. Nat. Mosc. 252: 320. 1852. Exolobus Fourn. in Mart. Fl. Bras. 64: 318. 1885. Trichostelma Baill. Hist. Pl. 10: 287. 1891. Lachnostoma of North American authors. The complications concerning the use of Gonolobus Michx. and Vincetoxicum Walt., the "temporary" conservation of Vincetoxicum Moench. over the latter, and the typification of Gonolobus by G. gonocarpos (Walt.) Perry have been discussed in previous paragraphs (p. 213). It may be remembered that the original element of Vincetoxicum Walt. (or Gonolobus, through the rejection of the earlier name) consists of two species, G. gonocarpos (Walt.) Perry, the type, and G. carolinensis (Jacq.) Schultes (V. acanthocarpos Walt.). Until recently no question has been raised against the consideration of these two species as congeneric, and Gonolobus became the general catch-all for gonoloboid species without sufficiently striking innovations of the corona to prompt their

WOODSON-NORTH AMERICAN ASCLEPIADACEAE. I 239

designation as separate genera. At about the opening of the present century, however, the earlier Vincetoxicum Walt. was revived by Dr. Britton and Miss Vail at the New York Botanical Garden. Transfers from Gonolobus were then in order, and few species of the complex have been described for that genus since. It seems rather severe that American botanists now will have to adjust themselves anew to the conservation of the dubiously valid Vincetoxicum Moench of Europe. In 1933 (in Small, Man. Fl. 1076.) E. J. Alexander separated G. gonocarpos and G. carolinensis generically, founding the genus Odontostephana with the latter, together with other species from the southeastern United States. Alexander quite naturally used Vincetoxicum Walt. in place of Gonolobus, the judgment of the authorities at Kew not yet having been passed. The key characters used to separate Vincetoxicum from Odontostephana were taken from the coronas, whether "Crown disk-like or saucer shaped, obscurely if at all ridged," or "Crown cup-shaped or incurved at the tip, usually crested or appendaged on the inner side." In the descriptions of the two genera, attention was called also to the characters of the fruits, longitudinally winged in the former, and muricate in the latter, as observed by Walter in 1788. It is regrettable that Odontostephana is antedated by Tetracustelma Baill. if a narrow generic concept is adopted, and that a broad concept will submerge it in Matelea Aubl. I have tried in vain to find characters of the corona which will separate Gonolobus and Matelea, but the structures of the anthers of the two genera appear to me as amply sufficient for distinction. The anthers of both vary considerably in size, position relative to the anther head, hyaline apical appendage, and nature of the marginal "wings." But in the species that I have assigned to Gonolobus the anther proper bears a more or less conspicuous, fleshy, usually laminate dorsal appendage which I never have found indicated to any degree in species assigned to Matelea. These dorsal appendages vary greatly from species to species, and although rather poorly developed as a rule in the temperate representatives, are very conspicu-

240 ANNALS OF THE MISSOURI BOTANICAL GARDEN

ous in the tropics. Typically, they are somewhat reniform in outline, but frequently deeply 2-lobed or entire, and rarely cleft into three divisions. The dorsal anther appendages are indicated in Alexander's figure for *Vincetoxicum* Walt. (loc. cit. 1933), although their significance is not mentioned, and a splendid illustration of them is provided by Baillon (Hist. Pl. 10: 235. fig.177. 1891) for G. erianthus.

The dorsal anther appendages of *Gonolobus* have been overlooked in most species of North America, but they were made the chief foundation for the genus *Exolobus* by Fournier (cf. Mart. Fl. Bras. 6^4 : *pl.94*. 1885), who designated them as "corona superior." The species assigned to *Gonolobus* by Fournier all are of the element represented by *G. hirsutus* Michx. which I am relegating to *Matelea*. K. Schumann (in Engl. & Prantl, Nat. Pflanzenfam. 4^2 : 298, 301–302. 1895) followed Fournier in the separation of *Gonolobus* and *Exolobus*, but appears to have been remarkably confused, for the dorsal anther appendages of my terminology are described as "inner corona" ("corona . . . innere an den A. befestigt, nach aussen strahlend, fleischig.") for the former, but for the latter simply as appendages of the anthers ("Stb. mit einem mitt-

leren, fleischigen, nach aussen gerichteten Fortsatze. . .'').

As I have explained previously (p. 199), flowers of Gonolobus as interpreted in this paper customarily have three structures which may be called "corona" if the terminology is loose: a corolline faucal annulus, frequently ciliate, a fleshy true corona borne at the base of the staminal column, and the dorsal appendages of the anthers proper. In his key to the Gonolobeae, Schumann (loc. cit. 298) places both Gonolobus and Exolobus under the division "II. Corona doppelt," and distinguishes them by "1. Äussere Corona kahl" and "2. Äussere Corona gewimpert," respectively, apparently referring to the corolline annulus.

In his descriptions of the two genera, however, Schumann reveals by his ambiguity how confused was his concept: "Corona ringförmig, einfach oder doppelt, die äussere zuweilen noch von einem häutigen Rande umgeben, so dass man fast 3

WOODSON-NORTH AMERICAN ASCLEPIADACEAE. I 241

Coronen unterscheiden kann, oft ringförmig, der Blkr. angeheftet, kurz, gestutzt oder gelappt, zuweilen durch 5 Gewebeplatten mit dem Gynostegium verbunden; innere an den A. befestigt, nach aussen strahlend, fleischig" (Gonolobus, p. 301); "Corona doppelt: äussere in der Form eines sehr niedrigen, behaarten, aus den Blkr. vortretenden Ringes, die innere aus 5 freien Schuppen bestehend, welche der Röhre des Gynostegiums angeheftet sind. Stb. mit einem mittleren, fleischigen, nach aussen gerichteten Fortsatze und einem häutigen Mittelbandanhang" (Exolobus, p.302). The coup de grace is given these verbal circumlocutions by a consideration of fig. 92, N-T, provided by Schumann (p.301) to illustrate Gonolobus and Exolobus. The floral structures are found to be equivalent in all important particulars, even to a "gewimpert corona" (ciliate corolline annulus) for G. riparius. The extended quotations from Schumann should be sufficient to illustrate the ambiguity that results from treating the term "corona" in a complex sense. The dorsal anther appendages of Gonolobus are not equivalent to any structure found in Matelea. At one time during these studies, I suspected that they might represent the adnation to the anther of the inner ligules commonly accompanying the corona segments of the latter genus. This is shown to be erroneous, however, by the fact that these ligules almost invariably occur in Gonolobus in addition to the dorsal anther appendages, which apparently are more directly comparable to the vesicular tissue of the anthers of Fischeria. I am not yet sufficiently informed to know positively what will result when this character is applied extensively to the South American gonoloboids, but wide observations indicate its validity. Supporting characters are found amongst the relatively few species of Gonolobus and Matelea for which fruit is known, the follicles of the former being longitudinally winged, infrequently quite smooth, and those of the latter muricate or infrequently smooth. The smooth condition would appear to be derived from both series. In Matelea, as has been explained previously, a peculiar indument of eglandular and

242 ANNALS OF THE MISSOURI BOTANICAL GARDEN

interspersed glandular hairs characteristically occurs; such an indument never is found in Gonolobus.

Amongst the North American species of Gonolobus with which I am familiar at present, the following divisions into subgenera appear both natural and convenient. As usual, I have illustrated them with necessary transfers.

KEY TO SUBGENERA

- A. Corolla with widely spreading or reflexed lobes, with a more or less pronounced faucal annulus exterior to the true corona.
 - B. Anthers only about half included beneath the broadly 5-gonal stigma
- BB. Anthers wholly (except the dorsal appendages) included beneath the
- AA. Corolla with erect or ascending lobes, without a faucal annulus......

I should like to include Trichostelma Baill. in this key either as a subgenus or as a section under Eugonolobus, but the height of the corolline annulus appears to be far too variable.

SUBGENUS 1. PTEROLOBUS

GONOLOBUS chiapensis (Brandg.) Woodson, comb. nov. Vincetoxicum chiapense Brandg. Univ. Cal. Publ. Bot. 6: 190. 1915.

In addition to the preceding, Pterolobus includes such species as G. niger R.Br., G. Salvinii Hemsl., and G. nemorosus Done. The name refers to the undulated wings of the follicles of the few species where I have observed them.

SUBGENUS 2. EUGONOLOBUS

GONOLOBUS albomarginatus (Pittier) Woodson, comb. nov. Exolobus albomarginatus Pittier, Contr. U.S. Nat. Herb. 13: 108. fig.16. 1910.

GONOLOBUS aristolochiaefolius (Brandg.) Woodson, comb. nov.

Fischeria aristolochiaefolia Brandg. Univ. Cal. Publ. Bot.

6: 190. 1915. GONOLOBUS calycosus (Donn.Sm.) Woodson, comb. nov. Trichostelma ciliatum Baill. Hist. Pl. 10: 288. 1891, non G. ciliatus Schltr.

243 WOODSON-NORTH AMERICAN ASCLEPIADACEAE. I

Fimbristemma calycosa Donn.Sm. Bot. Gaz. 16: 196. pl. 16. 1891.

GONOLOBUS cteniophorus (Blake) Woodson, comb. nov. Vincetoxicum cteniophorum Blake, Contr. Gray Herb. 52: 84. 1917.

Vincetoxicum ? tortum Brandg. Univ. Cal. Publ. Bot. 10: 414. 1924.

Vincetoxicum Lundellii Standl. Field Mus. Publ. Bot. 8: 148. 1930.

GONOLOBUS dasystephanus (Blake) Woodson, comb. nov. Vincetoxicum dasystephanum Blake, Contr. Gray Herb. 52: 84. 1917.

GONOLOBUS Lasiostemma (Hemsl.) Woodson, comb. nov. Lachnostoma Lasiostemma Hemsl. Biol. Centr.-Am. Bot. 2: 335. 1882.

GONOLOBUS oblongifolius (Donn.Sm.) Woodson, comb. nov. Trichostelma oblongifolium Donn.Sm. Bot. Gaz. 48: 296. 1909.

GONOLOBUS stenanthus (Standl.) Woodson, comb. nov. Vincetoxicum stenanthum Standl. Field Mus. Publ. Bot. 4: 255. 1929.

GONOLOBUS stenosepalus (Donn.Sm.) Woodson, comb. nov. Fimbristemma stenosepala Donn.Sm. Bot. Gaz. 18: 208. 1893.

SUBGENUS 3. PSEUDOLACHNOSTOMA GONOLOBUS arizonicus (A.Gray) Woodson, comb. nov. Lachnostoma arizonicum A.Gray, Proc. Amer. Acad. 20: 296. 1885.

GONOLOBUS gonoloboides (Greenm.) Woodson, comb. nov. Lachnostoma gonoloboides Greenm. Proc. Amer. Acad. **39**: 84. 1903.

IX. MARSDENIA R.Br. Mem. Wern. Soc. 1: 28. 1809.

Nephradenia Dcne. in DC. Prodr. 8: 604. 1844. Ecliptostelma Brandg. Univ. Cal. Publ. Bot. 6: 371. 1917. I have been unable to find characters to distinguish Nephradenia except the erect, fruticose habit. Ecliptostelma molle

244 ANNALS OF THE MISSOURI BOTANICAL GARDEN

Brandg. (loc. cit. 1917) is identical with Marsdenia Gilgiana Rothe, which seems to be an extraordinarily variable species, even from the present meager representation, and which possibly should be merged with the very closely neighboring M. *mexicana* Dcne. For further generic synonyms, reference should be made to the monograph by Rothe (in Engl. Bot. Jahrb. 52: 354-434. 1915). Following that standard work, new sections or subgenera probably will have to be erected to include both the following species, although I am deferring that action for the present.

MARSDENIA astephanoides (A.Gray) Woodson, comb. nov.
Vincetoxicum astephanoides A.Gray, Proc. Amer. Acad.
22: 435. 1887.

Cynanchum astephanoides (A.Gray) Standl. Contr. U.S. Nat. Herb. 23: 1177. 1924.

MARSDENIA neriifolia (Dcne.) Woodson, comb. nov.

Blepharodon neriifolium Dcne. in DC. Prodr. 8: 604. 1844.

Nephradenia neriifolia (Dcne.) Benth. & Hook.; Hemsl. Biol. Centr. Amer. Bot. 2: 336. 1882.

Nephradenia fruticosa Donn. Sm. Bot. Gaz. 16: 196. 1891.

